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MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

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A NEW CLASSIFICATION OF THE TRIBE CICHORIEAE, FAMILY COMPOSITAE

G. Ledyard Stebbins, Jr.

Introduction

The monumental monograph of the genus *Crepis* by Babcock (1947) showed brilliantly how newer information from genetics, cytology, and distribution can be integrated with the more classical discipline based on gross morphology to produce a natural classification of a large group of plants, and to gain added insight into its interrelationships and evolution. From 1935 to 1939, the present writer was engaged in a study of the relatives of *Crepis,* in order to make clear the position of this genus in its tribe and family. Essentially the same techniques were employed as those used by Babcock, except that hybridizations were not attempted. Since the genera of the tribe Cichoriae are so remotely related to each other that few intergeneric hybrids involving them have ever been obtained, hybridization attempts would contribute little to a clarification of intergeneric relationships.

The writer's studies led him rather quickly to the conclusion that the accepted classification of the tribe Cichorieae, namely that by Hoffmann (1891) in "Die naturlichen Pflanzenfamilien," is artificial in many respects, and that a new classification of the tribe is needed. The present attempt was made in conjunction with a survey of the chromosome numbers in the tribe, which is published elsewhere (Stebbins, Jenkins and Walters, 1953).

Previous Classifications of the Tribe Cichorieae

The Cichorieae, or Cichoriaceae, were first recognized as a natural group ("Ordo") by de Jussieu (1789) and since that time have always been considered as the most distinctive and easily recognizable subdivision of the family Compositae, or by some authors as a separate family. On the other hand, different systems of classification have varied greatly in their subdivision of the tribe. Jussieu recognized five subdivisions, but defined them rather poorly. Nevertheless, he used the two characters, namely presence or absence of receptacular paleae, and character of the pappus, which have by all more recent authors been regarded as the most important diagnostic characters. Don (1825) made an entirely different arrangement of the genera, using in addition to the characters of Jussieu, also the character of the involucre, of the anther appendages, and of the stigmas. His system is particularly artificial in respect to his tribes Hypochaerideae and Lactuceae. The former contains the modern genus *Hypochaeris,* plus two species, placed in the genera *Agenora* and *Soldevilla,* which are now recog-

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nized as species of *Crepis*. The bulk of *Crepis* is placed in the tribe Hieracieae, while *Leontodon* and *Picris*, the nearest relatives of *Hypochaeris*, are placed by Don in the tribe Taraxaceae. Don's tribe Lactuceae contains, besides genera now included in *Lactuca* and *Sonchus*, also *Chondrilla*, *Lygodesmia*, and *Barkhausia*, of which the latter "genus" is now united with *Crepis*.

The next treatment, that of Lessing (1832) recognized seven subtribes, which in many respects resemble those of the well-known later treatment by Hoffmann. Lessing, however, placed as much emphasis on the presence or absence of receptacular paleae as he did on the nature of the pappus, and attempted to distinguish between those genera having a fine, caducous pappus on the one hand, and those with a coarse, persistent pappus on the other. As a result, he separated the modern genus *Hypochaeris* into a separate subtribe from its close relatives *Leontodon* and *Picris;* and divided the genus *Crepis*, as recognized by modern authors, into several "genera," which are distributed between the subtribes Lactuceae and Hieracieae. DeCandolle (1838) recognized Lessing's seven subtribes, and added an eighth, the Rodigieae, an entirely artificial aggregation of groups with a paleaceous receptacle and a capillary, non-plumose pappus.

George Bentham, one of the outstanding students of the Compositae of the last century, made no attempt to subdivide the tribe Cichorieae. In Bentham and Hooker's Genera Plantarum (1872) the genera are listed without subtribe headings. Bentham followed the same course in his (1873) discussion of the phylogeny and geographic distribution of the Compositae, though he did suggest intergeneric relationships in discussing geographic distribution.

Finally Hoffman (1891) made the systematic arrangement best known to present day botanists, and the one on which the treatment in most modern floras is based. He recognized five subtribes. The first, the Scolyminae, agreeing with that of Lessing, contains only the genus *Scolymus*. The second, the Dendroseridinae, was erected for two anomalous arboreal insular genera, *Dendroseris* of Juan Fernandez, and *Fitchia* of the South Sea Islands. The Cichorinae unites the Hyoserideae and Lampsaneae of Lessing, so as to include all of those genera with paleaceous or coroniform pappus, or with epappose fruits. The Leontodontinae unites the Hypochaerideae and Scorzonereae of Lessing, including all genera with the pappus consisting of plumose bristles. Finally, the Crepidinae of Hoffmann unites the Lactuceae and Hieracieae of Lessing, and includes all genera with capillary, non plumose pappus.

Hoffmann's system, therefore, differs from Lessing's in little except in the fact that Hoffmann does not consider either the differences between the presence or absence of a pappus, or between the presence or absence of receptacular paleae, to be of subtribal significance. Hoffmann's system, therefore, is based almost entirely upon a single character, the nature of the pappus.

The artificiality of such a system has been brought out strikingly by the writer's studies of pollen grains, stigmas, and particularly chromosomes, in conjunction with geographic distribution and the general growth habit of the plants. This artificiality is particularly evident in the genera of the New World. An example is the complex consisting of *Microseris* (including *Scorzonella* and *Uropappus*), *Apargidium, Agoseris,* and *Phalacroseris.* All of these genera agree in having short thick stigma branches, a peculiar orange color to the mass of pollen grains, and eighteen chromosomes, except for occasional polyploids. In the long-lived perennial species of these genera, the chromosomes are all similar in size and shape. Furthermore, the species resemble each other in general growth habit, and all have their main distribution in western North America. Yet the pappus in *Microseris* is paleaceous; in *Apargidium* it consists of coarse, fragile, dark colored bristles; in *Agoseris* it consists of white bristles, which may be either coarse or fine; while in *Phalacroseris* it is absent. The connection between *Microseris* and *Agoseris* is particularly close. *Microseris troximoides,* which has numerous very narrow pappus paleae, is closely similar in general habit of growth to *Agoseris cuspidata,* in which the pappus consists of very coarse trichomes, hardly different from the paleae of *M. troximoides.* Yet Hoffmann places *Microseris,* along with *Phalacroseris,* in the Cichorinae, while *Agoseris* and *Apargidium* are placed in the Crepidinae.

In other places, Hoffmann appears to contradict his own classification. Thus *Zacyntha* and *Heteracia* are both placed in the Cichorinae along with genera having a paleaceous pappus, although in both the pappus is described in the generic description as "borstig." Babcock (1947) after careful study of the single species of the genus *Zacyntha,* concluded that the genus should be merged with *Crepis,* while the writer's study of *Heteracia* has shown that it belongs in the Crepidinae near to *Chondrilla,* which it resembles closely in involucres and achenes.

POSITION OF THE TRIBE CICHORIEAE

In the opinion of the present writer, the Cichorieae should be treated, as they are by most systematists, as a tribe of the family Compositae, rather than as a separate family. The latter treatment is unwise for two reasons. In the first place, the morphological gap between the Compositae as a whole and any other plant family is far greater than that between the Cichorieae and the rest of the Compositae. Secondly, there are a few genera which form partial transitions between the two groups. Within the tribe Cichorieae itself, the genus *Scolymus* resembles the Cynareae in its thistle like habit of growth, and in possessing oil ducts. *Gundelia,* an anomalous genus of the *Arctotidae,* agrees with *Scolymus* in its thistle like growth habit, and in possessing latex canals as well as oil ducts. The ligulate corolla, which is so distinctive a characteristic of the Cichorieae, is found also in *Stokesia* of the Vernonieae and in some genera of Mutisieae. Finally the echinolophate pollen grain, another characteristic distinctive of most genera of Cichorieae, is found also in the Vernonieae. There is, therefore, no single characteristic found in the Cichorieae which does not occur in other genera of Compositae.

On the other hand, the Cichorieae cannot be allied to any other single tribe of Compositae. In corolla shape they are nearest to the Mutisieae; in anthers, stigmas, and pollen grains they are nearer to the Vernonieae. They resemble both of these tribes in having alternate leaves, and in the general character of their involucres. But there are no direct connections between the Cichorieae and either the Vernonieae or Mutisieae, so that the similarities observed may not indicate any real relationship. The best assumption at present is that the ancestors of the Cichorieae became separated from the ancestors of the rest of the Compositae at a very early date in the evolution of the family, before the present day tribes had become well defined.

Characters Used in the Present Study

As have all previous workers, the writer has found the pappus to be the most useful single character for subdividing the tribe. Nevertheless, as has been mentioned above, it cannot be used as a major diagnostic character in all instances, since there are several examples of genera which are closely similar in all other respects but differ in the nature of their pappus. In particular, the absence of a pappus is a very poor criterion of affinity, since this structure seems to have been lost in several different and independent lines of evolution. Consequently, the epappose genera placed by Lessing in the Lampsaneae and by Hoffmann in the Cichorinae, have by the present writer been scattered elsewhere through the system, according to the position of the genera which they most nearly resemble in other characteristics.

The morphological characters most valuable next to the pappus are the shape of the stigma branches and the character of the pollen grains. In nearly all genera of Cichorieae native to the Old World, the stigma branches are long and slender, but in most of the genera endemic to the New World, they are short and blunt. In respect to pollen grains, the Old World genera nearly all have grains bearing the pattern of surface markings characterized by Wodehouse (1935) as echinolophate, and consisting of ridges bearing spines. In many of the New

World genera of Cichorieae, on the other hand, the pollen grains are merely echinate, as they are in most of the other tribes of Compositae.

An accessory character which has been helpful in many instances is the nature of the indumentum on the plant as a whole. Four different types of trichomes occur in the various genera of the tribe. Those found most often, and present on some part of the plant of nearly every species, are slender, appressed, usually crisped and often much elongated hairs, which may form either a fine or coarse and arachnoid tomentum. Next in frequency are spreading hairs, which vary from rather fine structures to coarse, broad-based bristles. These give a hirsute character to the plant. They are found in the majority of the Old World genera, but are absent from nearly all of the genera endemic to the New World. The third type are coarse, spreading, trichomes which are forked or stellate at the apex. These are best developed in the genus *Leontodon,* but occur also in other Leontodontinae. Finally, there occur coarse, spreading trichomes with glands at the apex. These are usually confined to the peduncles and involucres. Although the occurrence of a particular type of indumentum can never be used as a primary diagnostic character of a tribe or genus, nevertheless genera which resemble each other in general habit, in geographic distribution, and in their chromosomes often have a similar indumentum, so that this character can be used to supplement other characters.

As in the genus *Crepis* itself, the karyotype has in many instances proved to be a valuable clue to the affinities of the various genera. The basic haploid chromosome number has proved to be the most valuable, followed by the size. The morphology of the somatic chromosomes is in general more valuable in determining the relationships of species within a genus, than the position of genera within the tribe.

Differences Between the Present Classification and Previous Ones

The principal difference between the present classification of the tribe Cichorieae and those previously proposed is that the present writer has not distributed the genera into a few major subdivisions based on one or two easily recognized "key characters," but has considered each genus separately, placing it nearest to those genera which it most nearly resembles in respect to the largest number of characteristics of external morphology, plus the nature of the chromosomes and the geographic distribution. In addition, genera have been placed near each other if they are connected by transitional species, even if the most typical species of the genera concerned are very different in a number of characteristics. An example of this treatment is the placing of *Microseris* and *Agoseris* next to each other. This method has resulted in a classification which cannot be expressed in the form of an artificial key, since the character combinations which characterize the major subdivisions are often difficult to determine on the usual type of herbarium specimen available. For this reason, no artificial keys to subtribes or to genera have been attempted. In his work of identification, the writer has found that the keys used in the various regional floras and manuals are quite adequate for identification purposes, even though they often do not place related genera next to each other.

The chief innovation by the present writer has been the erection of two new subtribes endemic to the New World, the Stephanomerinae and Malacothricinae. This has been the direct outcome of the emphasis on chromosomes and geographic distribution plus consideration of pollen grain and stigma characters. The reasons for this treatment will be discussed below.

SUBDIVISIONS OF THE TRIBE CICHORIEAE

The tribe Cichorieae can be divided into eight subtribes, as follows:

SUBTRIBE 1. **Scolyminae.** Plants thistle-like; receptacle with broad, chaffy paleae which enclose the achenes; oil ducts as well as latex canals present; pappus of a few, coarse bristles; pollen grains echinolophate. Basic chromosome number, x=10. One genus, *Scolymus,* Mediterranean. The isolated position of this genus, which has been placed in a subtribe by itself by all previous workers, is borne out by its chromosome number, which is different from the basic number of any other genus in the tribe. In the thistle-like habit, as well as in the possession of oil ducts, *Scolymus* is transitional toward genera of the Cynareae and Arctotidae.

SUBTRIBE 2. **Cichorinae.** Plants various in habit, but usually bearing coarse, broad based, non-glandular trichomes; receptacle paleaceous in *Hymenonema,* bristly in *Catananche,* glabrous in the other genera; flowers blue or yellow; achenes (except in *Koelpinia*) short, turbinate or columnar, truncate at the apex; pappus usually consisting of paleae or awns, or absent, bristly only in *Tolpis;* pollen grains echinolophate, the pollen mass pale yellow in color; stigma branches mostly elongate. Basic chromosome number in most genera x=9, in *Hyoseris* x=8, unknown in *Hymenonema, Haenseleria,* and *Hispidella.* Nine genera, all primarily Mediterranean, with *Tolpis* extending to central and south Africa, with *Koelpinia* extending to central Asia, and with species of *Cichorium* and *Arnoseris* occurring in many regions as introduced weeds. The following genera are included: *Hymenonema, Catananche, Cichorium, Haenseleria, Tolpis, Hispidella, Arnoseris, Koelpinia, Hyoseris.*

This subtribe is a relatively small one, since only two of its genera, *Cichorium* and *Tolpis,* with seven to eight and fifteen to twenty species respectively, contain more than five species. It is, furthermore, a relatively heterogeneous subtribe. The genera *Hymenonema, Catananche,* and *Cichorium* are all rather closely related to each other, as are also *Tolpis, Hispidella, Arnoseris,* and probably *Koelpinia.* But these two groups of genera have relatively little in common, and in fact *Tolpis* and its relatives appear in many respects to be related to *Hieracium* of the subtribe Crepidinae. The small genera *Haenseleria* and particularly *Hyoseris* occupy isolated positions, showing no clear relationships to any other genus.

SUBTRIBE 3. **Microseridinae.** Plants mostly low in stature, tending to be acaulescent or with few heads per stem; mostly glabrous, sometimes appressed tomentose, rarely with a few glandular hairs, but never hirsute; receptacles never paleaceous or setose; flowers yellow; achenes various in shape; pappus of paleae, awns, setae, or absent; pollen grains echinolophate, the pollen mass bright orange in color; stigma branches short and blunt. Basic chromosome number $x=9$, $x=6$, and $x=5$. Seven genera, all except *Picrosia* predominantly or entirely North American, with *Agoseris* and *Microseris* containing species in South America, and one species of *Microseris* in Australia. The writer follows Shinners (1947) in uniting *Serinia* with *Krigia.*
Contains the following: *Microseris, Phalacroseris, Apargidium, Agoseris, Krigia, Pyrrhopappus,* and *Picrosia.*

The recognition of this subtribe is based primarily on the fact that the first four genera mentioned are closely similar in general habit of growth, geographic distribution, and chromosomes, and are connected by transitional species. The only technical characters which separate them from the Cichorinae are the short, blunt, and rather broad stigma branches, and the peculiar orange color to the pollen mass, which is due to the presence in the anthers of some sort of oily or fatty substance. *Krigia* and *Pyrrhopappus* share with these four their pubescence, stigma, and pollen characters, and are likewise North American, although they occur on the eastern rather than the western side of that continent. The monotypic genus *Picrosia,* of eastern temperate South America, is closely related to *Pyrrhopappus,* of which it is probably a specialized offshoot.

SUBTRIBE 4. **Stephanomerinae.** Plants varying in habit from shrubs to small annuals; mostly glabrous, but some species appressed-tomentose, none hirsute with spreading hairs; receptacle paleaceous in *Pinaropappus,* bristly in some species of *Malacothrix,* naked in the other genera; flowers pink, white, or less often yellow; achenes cylindric, fusiform, or beaked, never flattened; pappus setose (absent in *Atrichoseris*), the setae either plumose or non-plumose; pollen grains echinate, except in three or four species of *Lygodesmia;* stigma branches mostly short. Basic chromosome numbers x=9, 8, 7, and 6. Eleven genera, all North American (except for *Thamnoseris*): *Stephanomeria, Chaetadelpha, Lygodesmia, Thamnoseris, Pinaropappus, Malacothrix, Rafinesquia, Anisocoma, Calycoseris, Glyptopleura, Atrichoseris.*

The genera of this subtribe are rather diverse in both general habit and technical characters, and there is no single diagnostic character by which they can be distinguished. The great majority of the species differ from all of the Old World species and genera to which they have previously been related by their echinate pollen grains, the pollen grains of the Old World genera being echinolophate except for some species of *Soroseris* (Stebbins, 1940). This character breaks down, however, in *Lygodesmia,* since *L. runcinata, L. grandiflora, L. aphylla,* and *L. texana* all have echinolophate pollen grains. A second character is that in most species of the Malacothricinae the stigma branches are shorter than in most species of the Leontodontinae, Scorzonerinae, and Crepidinae, the Old World subtribes in which they might be placed. But in species of *Pinaropappus* and *Lygodesmia* the stigma branches are distinctly elongated, while in some Old World species they are relatively short.

Nevertheless, these New World genera have certain features of general habit which relate them individually to each other more closely than any of them appear to be related to genera of the Old World. For instance *Stephanomeria,* with plumose pappus bristles, appears to be more similar to *Lygodesmia,* which has non-plumose bristles, than to any genus of the Leontodontinae, in which it is placed by Hoffmann. Similarly the plumose bristled *Anisocoma* resembles the annual species of *Malacothrix* more than any species of Leontodontinae. If these genera with few and stout, plumose pappus bristles were placed into the Crepidinae along with the apparently related North American genera having numerous, slender non-plumose bristles, then the chief distinction between the Leontodontinae and Crepidinae would disappear. Since these New World genera do not seem in other characters to represent intergrades between the Old World Leontodontinae and Crepidinae, but rather independent evolutionary lines which are offshoots from some extinct common ancestor, their recognition as a separate subtribe fits best with their probable phylogenetic relationships. Their chromosomes bear out this treatment. Although diverse in both basic chromosome number and chromosome morphology, the karyotypes of these genera do not resemble those of any genera of Leontodontinae or Crepidinae.

Two rather different groups of genera can be recognized in the subtribe Stephanomerinae. One, consisting of *Stephano-*

meria, *Lygodesmia*, and *Chaetadelpha*, contains plants which are usually much branched, with leaves reduced in size, and with narrow heads containing few florets. Shinners (1950) has recently merged *Stephanomeria* with *Lygodesmia*, but in the writer's opinion these two genera are no closer to each other in the sum total of their habital and floral characteristics than are many other pairs of generally recognized genera of the Cichorieae. In addition to the pappus, differences exist between most species of the two genera with respect to the character of the pollen grains, the length of the stigma branches, and the size and shape of the achenes. The little known genus *Thamnoseris*, endemic to the small islands San Felix and San Ambrosio, off the coast of Chile, appears related to this group. Although its geographic distribution is near to that of *Dendroseris*, *Thamnoseris* appears to have cylindric achenes like those of *Stephanomeria* rather than the irregular, strongly flattened type of achene characteristic of *Dendroseris*, and so does not fit well into the Dendroseridinae. The small genus *Rafinesquia*, of the southwestern United States, although somewhat isolated in position, is probably nearer to *Stephanomeria* than to any other genus, and agrees with *Stephanomeria* in having the basic chromosome number $x=8$.

The second group of genera contains *Malacothrix* plus four small genera of the southwestern deserts, *Anisocoma*, *Atrichoseris*, *Calycoseris*, and *Glyptopleura*. These are all annual herbs except for three or four species of *Malacothrix*. They are relatively little branched, and have heads with numerous florets. The remaining genus of the subtribe, *Pinaropappus*, resembles *Stephanomeria* in general habit, but in its many flowered heads is more like *Malacothrix*. It is, however, wholly distinctive among New World genera of the Cichorieae in its paleaceous receptable and strongly beaked achenes, while it is the only genus of the tribe of which the distributional center is in Mexico.

SUBTRIBE 5. **Dendroseridinae.** Shrubs or trees up to seven meters tall, with large, entire or pinnatifid leaves. Inflorescences and involucres very diverse in appearance and size; receptacle naked; flowers mostly white; achenes irregular in shape, flattened; pappus of relatively few, coarse, non-plumose setae; pollen grains echinate; stigma branches short or somewhat elongated. Basic chromosome number, $x=9$. One genus, *Dendroseris*, endemic to the Juan Fernandez islands.

The genus *Dendroseris* resembles the Stephanomerinae in most of its characteristics, particularly its pollen grains, and is probably a specialized offshoot from some primitive member of that tribe. Nevertheless, its distinctive habit and peculiar achenes set it off so well from any living genus of Stephanomerinae, with the possible exception of *Thamnoseris*, that the best course is to follow Hoffmann and place it in a separate tribe. This treatment is supported by the chromosome studies. The species of *Dendroseris* investigated have in their somatic cells thirty-six small chromosomes, very different in appearance from those of any other New World member of the Cichorieae.

Skottsberg (1951) has recently suggested that *Dendroseris* should be divided into four genera, two of which he describes as new. He has based this decision partly upon their great diversity in certain characters of external morphology, and partly upon characters of the pollen grains, provided by Wodehouse and Erdtman. In the writer's opinion, this splitting is unwise. The diversity in external morphology among the species of *Dendroseris* is no greater than that found within many genera of the Compositae, and less than that in *Sonchus* and *Lactuca*. In respect to the pollen grains, the writer (Stebbins, 1940) showed that the two sections of the central Asiatic genus *Soroseris* have pollen grains which differ from each other to about the same degree as those of the sections of *Dendroseris* which Skottsberg proposes to recognize as genera. In *Prenanthes,* the central African species *P. subpeltata* has pollen grains which differ from those of typical *Prenanthes* more than the sections of *Dendroseris* differ from each other, and the same is true of the different sections of the American genus *Lygodesmia*. Hence none of the differences between the sections of *Dendroseris* would force us to recognize them as genera.

In the writer's opinion, the chief reason for recognizing new genera among well known species previously grouped together is different from any suggested by Skottsberg. If a particular group of species is well set off in respect to several characters from all other species of the genus to which it is traditionally assigned, and shows such clear relationships to other genera that it might as well be assigned to them, then its recognition as a distinct genus is well justified. This is true of the new genera of Cichorieae recognized by Babcock and the writer, as well of the old genera revived and redefined, such as *Youngia, Dubyaea, Soroseris, Aethiorrhiza,* and *Cicerbita*. But this is not true of the sections of *Dendroseris*. Although they appear distinct from each other in respect to a number of characteristics, they all resemble each other far more closely than any of them resembles any other genus of Cichorieae. This holds for chromosome number and morphology, so far as known, as well as for external characters. They are thus much more easily dealt with as a single unit than as four separate units with different names.

Hoffmann includes in the tribe Dendroseridinae also *Fitchia,* a genus of three species of arboreal Compositae endemic to certain islands of the South Pacific. After careful examination of excellent herbarium material of *Fitchia speciosa* in the herbarium of the University of California, the present writer agrees with those authors who consider that *Fitchia* does not belong in the tribe Cichorieae at all. The only character in which it resembles the Cichorieae is the ligulate corolla, and even here the resemblance is only superficial .The corolla of *Fitchia* is very deeply and irregularly lobed, with the lobes strongly pubescent at the apex. Furthermore, it is traversed by a complex system of vascular bundles, in striking contrast to the simple pattern of venation found uniformly throughout the Cichorieae. Actually, *Fitchia* contains a combination of characters not found in any other genus of Compositae, and has many very primitive features. In the writer's opinion, it should be placed in a tribe by itself, which shares characters of the Heliantheae and Mutisieae, two tribes which otherwise are nearly at opposite ends of the system of the Compositae.

SUBTRIBE 6. **Scorzonerinae.** Perennial, biennial, or annual herbs; glabrous or appressed-tomentose, never hirsute; leaves mostly linear or elliptic, and entire, their principal veins parallel; involucres rather large; receptable naked; flowers pink, white or yellow; achenes cylindric, fusiform, or beaked; pappus of elongate, coarse, strongly plumose setae; pollen grains echinolophate; stigma branches elongate. Basic chromosome numbers, x=7 and x=6. *Scorzonera, Tragopogon*, and *Torneuxia*, native to Eurasia and North Africa.

The Scorzonerinae differ from the Leontodontinae, in which they have been placed by Hoffmann, by their lack of hirsute pubescence, their relatively large and pale achenes, the elongate, interlaced trichomes or plumes on their pappus bristles, and particularly in their distinctive habit and leaves. There are no genera transitional between the Scorzonerinae and Leontodontinae. In fact, the most generalized species of *Scorzonera,* such as *S. divaricata* of Central Asia, resemble *Stephanomeria* and *Lygodesmia,* of the Stephanomerinae, in both habit of growth and adaptation to xeric habitats, as well as in their achenes. The Scorzonerinae are certainly a specialized group, but appear to have been derived from some group nearer to the Stephanomerinae than to the Leontodontinae or their ancestors.

SUBTRIBE 7. **Leontodontinae.** Perennial or annual herbs, mostly with coarse, spreading, hirsute pubescence, the hairs often forked; involucres various in size and appearance; receptacle paleaceous or naked; flowers nearly always yellow; achenes mostly fusiform or beaked; pappus of coarse, plumose setae, or occasionally paleaceous or coroniform; pollen grains echinolophate; stigma branches elongate. Basic chromosome numbers, x=7, 6, 5, 4, and 3. Seven genera, all predominantly Mediterranean, with *Hypochaeris* extending to eastern Asia and South America, *Picris* to eastern Asia, and with species of nearly all of the genera introduced as weeds into various regions of the world. Includes the following: *Hypochaeris, Leontodon, Picris, Urospermum, Hedypnois, Garhadiolus, Rhagadiolus.*

As recognized here, the Leontodontinae are a relatively small, closely knit group. In general habit as well as distribution, they resemble certain genera of the Crepidinae, particularly *Hieracium* and *Crepis.* This resemblance also extends to the pollen grains, stigmas, and chromosomes. Nevertheless, there is little reason to believe that the modern Crepidinae are descended from the modern Leontodontinae or vice versa. As will be pointed out below, most of the genera of Crepidinae can be traced back, on the basis of evidence from both external morphology and chromosomes, to the genus *Dubyaea,* which in all respects except for its receptacle and pappus is more primitive than any genus of Leontodontinae. The most primitive genus of this latter tribe, *Hypochaeris,* because of its paleaceous receptacle and few, course pappus bristles, cannot be derived from *Dubyaea* or any other genus of Crepidinae. Furthermore, the coarse, often forked trichomes which form the most common type of indumentum in the Leontodontinae are found more often in the Cichorinae than the Crepidinae, and suggest a connection between the Leontodontinae and the Cichorinae.

The writer has transferred to the Leontodontinae three small genera which Hoffmann placed in the Cichorinae, namely *Hedypnois, Garhadiolus,* and *Rhagadiolus.* The most primitive species of these genera resemble *Leontodon* and *Picris* in growth habit, involucres, and achenes, as well as chromosome number and morphology. Hoffmann placed them in the Cichorinae because their pappus is mostly paleaceous, coroniform, or absent, rather than consisting of plumose bristles. In *Leontodon,* however, there are several species in which the marginal achenes of the head have a paleaceous or coroniform pappus, whereas in certain species of *Hedypnois* and *Garhadiolus* the "paleae" composing the pappus are actually coarse bristles which may or may not be somewhat broadened at the base. *Rhagadiolus* is a highly specialized derivative of *Garhadiolus* in which the mature achenes and inner involucral bracts are much elongated, and the pappus has become lost.

SUBTRIBE 8. **Crepidinae.** Plants various in habit, from much reduced annuals to small trees; involucres and achenes likewise various; pappus of numerous coarse or fine non-plumose setae; stigma branches elongated; pollen grains echinolophate, except in *Soroseris* and one species of *Prenanthes.* Basic chromosome numbers x=9, 8, 7, 6, 5, 4, and 3. Twenty-five genera, all predominantly Eurasian except for *Launaea, Sonchus,* and *Dianthoseris,* which are chiefly or entirely in Africa; but with species of various genera widespread in all other continents and insular regions either as indigenous or introduced members of the flora.

The Crepidinae form by far the largest subtribe of the Cichorieae, since their species far outnumber those of all of the other subtribes put together. They are also the most diverse in every respect, and contain species with many primitive characteristics as well as highly specialized ones. In all of their morphological characteristics, the species of the central Asiatic genus *Dubyaea* are the most primitive of this subtribe, and furthermore, different species of *Dubyaea* show clear resemblances and apparent relationships to various large and well recognized genera of the Crepidinae, such as *Lactuca, Crepis, Youngia, Prenanthes,* and *Hieracium* (Stebbins, 1940). In each of these larger genera, there are certain primitive species which resemble *Dubyaea* in various ways, and other species which are progressively more specialized in respect to the vegetative and floral characteristics listed in the discussion section, and more characteristic of the genera to which they belong. Our present knowledge of the interrelationships of the genera of Crepidinae is, therefore, best expressed by recognizing a series of phylogenetic lines which radiate outward from the primitive genus *Dubyaea*. This genus and its relative *Soroseris,* which forms the first of the radiating lines, have both been carefully described in a previous publication (Stebbins, 1940). The remaining lines are as follows.

Launaea-Sonchus line. Contains *Launaea, Sonchus, Reichardia, Aethiorrhiza,* and *Dianthoseris*. *Launaea* and *Sonchus* are both relatively large genera of which the greatest concentration of species is in Africa. The boundary between them is obscure, and cannot be accurately established until the African species of both genera have been carefully studied. Some species placed in *Sonchus* by Fries (1925) such as *S. rarifolius* Oliv. et Hiern. and *S. nanus* Sond., have characteristics of involucres, achenes, and the vascular anatomy of the ovary which indicate that they almost certainly belong in *Launaea*. The position of the monotypic genus *Aethiorrhiza,* of which the only species, *A. bulbosa* (L.) Cass., has often been placed in *Crepis,* has been fully discussed by Babcock and Stebbins (1943). *Dianthoseris*, endemic to the high mountains of central Africa, may not be distinct from *Launaea*.

The most conspicuous diagnostic character of the genera in this group is the type of pappus, consisting of coarse setae mingled with very fine, slender ones. In growth habit, its most primitive genus, *Launaea*, differs greatly from any species of *Dubyaea,* and certain species of *Launaea* resemble in this respect species of *Lygodesmia*. Since species of the latter genus also have unequal pappus bristles, there is some possibility that the *Launaea-Sonchus* line represents a group intermediate between the Crepidinae and Stephanomerinae, although this is not evident at all from the characteristics of its largest genus, *Sonchus.*

Hieracium line. Contains the very large and widespread genus *Hieracium* plus *Andryala*, a small genus endemic to the western half of the Mediterranean region. The distinctive features of this line are the cylindric and truncate achenes, and the fragile, usually colored pappus setae.

Prenanthes-Lactuca line. Contains *Prenanthes, Faberia, Cicerbita, Cephalorrhynchus,* and *Lactuca.* The most primitive members of this line are mesophytic herbs adapted to forests or subalpine meadows in the cooler parts of Eurasia. The species are predominantly tall, leafy stemmed plants with numerous heads. As recognized by the present writer, *Cicerbita* consists of three species, *C. alpina* (L.) Wallr. of northern and central Europe, *C. Pancicii* (Vis.) Beauverd of the Balkans, and *C. abietina* (Boiss.) Stebbins of the Caucausus. It stands midway between *Prenanthes* and *Lactuca.* Another small genus, *Cephalorrhynchus,* contains four species of southeastern Europe and southwestern Asia. It is distinguished from *Lactuca* chiefly by its five-sided achenes, which are little or not all all compressed. The reasons for uniting *Mulgedium,* as recognized by Hoffmann, with *Lactuca,* are given elsewhere (Stebbins, 1937a). *Faberia* is very close to *Prenanthes*, and perhaps not distinct from that genus.

Youngia-Ixeris line. Contains *Youngia, Ixeris, Lapsana, Aposeris, Taraxacum, Chondrilla, Willemetia, Heteroderis, Heteracia,* and *Acanthocephalus.* This line is characterized by the glabrous or only slightly tomentose character of the plants, the differentiation of the involucral bracts into two markedly different series, the rather small achenes which in the last six genera are truncate and strongly tuberculate at the apex; and the small chromosomes. *Lapsana* and *Aposeris,* which are placed by Hoffmann in the Cichorinae, are regarded by the present writer as specialized offshoots of primitive members of the *Youngia-Ixeris* complex, in which the pappus is absent or much reduced. The reasons for keeping *Youngia* distinct from *Crepis* have been discussed by Babcock and Stebbins (1937), while Stebbins (1937b) has discussed the characteristics which relate *Ixeris* to *Youngia* rather than to *Lactuca,* with which genus it is united by Hoffman. The writer has elsewhere (Stebbins, 1937b) given his reasons for uniting the genera *Crepidiastrum* and *Paraixeris* with *Ixeris.* The genera *Heteracia* and *Acanthocephalus,* placed in the Cichorinae by Hoffmann, appear to the writer to be specialized offshoots of *Chondrilla.* The pappus of the inner achenes in *Heteracia* is setose, with setae similar to those of most genera of Crepidinae, while the inner achenes themselves are much like those of *Chondrilla* and *Heteroderis.* Although the best known species of *Acanthocephalus, A. amplexifolius* Kar. et Kir, has very anomalous involucres and achenes, *A. Benthamianus* Regel et Schmal. has involucres which when young are not very different from those of *Heteracia,* and its achenes are shaped like those of *Heteracia* and *Chondrilla.*

Crepis line. Contains only the large genus *Crepis.* The phylogeny and relationships of this genus have been thoroughly discussed by Babcock (1947), who has stated in full his reasons for merging with it the genera *Zacyntha, Rodigia,* and *Pterotheca,* which were recognized by Hoffmann.

Relationships Between the Subtribes

The amount of information which has been obtained on both morphological and cytological characteristics of the Cichorieae makes possible some suggestions as to the relationships between the subtribes of Cichorieae and of the trends of evolution which have taken place in the group. Most of the morphological and cytological criteria which serve as a basis for determining the relative primitiveness or advancement of a species or genus have been discussed by Babcock (1947, pp. 42–48; 1950) and by the present author (Stebbins, 1940; Stebbins, Jenkins, and Walters, 1953). If we go by these criteria, we find that there is no genus or species of Cichorieae which is primitive with respect to all of them. Some species of *Dubyaea* are primitive in all respects except that they lack receptacular paleae, and possess a pappus of numerous bristles, rather than of relatively few paleae. Other genera which are relatively primitive are *Hymenonema* of the Cichorinae, *Microseris,* of the Microseridinae, and *Hypochaeris* of the Leontodontinae. When we compare these four genera with each other we find that they have relatively little in common, and the interrelationships between them are difficult to see. This suggests that divergent evolution had already progressed a considerable distance in the tribe before these modern genera originated, so that we must postulate the former existence of a whole series of types which are now completely extinct. This conclusion is further supported by the fact that the most primitive modern genera are found in regions geographically remote from each other. *Hymenonema,* along with the peculiar and much isolated genus *Scolymus,* occurs in the Mediterranean region; *Hypochaeris* extends from this region into central Asia, with an outlying and certainly derived group of species in South America; *Dubyaea* is in east Central Asia; while *Microseris* is in western North America. Because of this situation, the construction of a phylogenetic chart for the tribe would be highly speculative and misleading.

We may nevertheless conclude from these studies that the general phylogenetic trends in external morphology and in the character of the chromosomes which Babcock has demonstrated to have occurred in *Crepis* have also probably been characteristic of the tribe Cichorieae as a whole. Furthermore, the fact that the highlands of Central Asia are centrally located with respect to the distribution of the tribe as a whole, as well as its most primitive genera supports Babcock's hypothesis that the entire tribe Cichorieae, as well as the genus *Crepis*, originated in this region.

The time when this tribe originated cannot be inferred with any reasonable degree of probability. Babcock (1947, p. 131) produced evidence that *Crepis* originated in the early or middle part of the Tertiary period. Since the evidence summarized in this paper indicates that the tribe had already gone a long course of evolution before *Crepis* appeared, the origin of the tribe Cichorieae can hardly be placed at later than the beginning of the Tertiary or the end of the Cretaceous period. Its early evolutionary history will always be more or less obscure because of lack of evidence concerning the extinct forms, while the later history of the subtribes and genera will be clarified only as they become studied in the intensive manner which Babcock has applied to *Crepis*.

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TAXONOMY AND CHEMISTRY OF THE WHITE PINES[1]

N. T. MIROV

TAXONOMY

The white pines comprise the section *Haploxylon* of the genus *Pinus*. According to Shaw (21), there are nineteen species of white pines. These he assigns to two subsections, *Cembra* and *Paracembra*. His subsections are further divided into groups of which five represent the white pines proper, and a sixth group, *Cembroides*, which represents the pinyon pines. Some botanists regard the white pines proper as a distinct genus separate from the pinyon pines, while others separate the section Haploxylon into three genera (15, p. 11–13). Shaw's classification of *Haploxylon* is as follows:

SUBSECTION CEMBRA

- Group Cembrae
  - *P. koraiensis* Sieb. & Zucc.
  - *P. cembra* L.
  - *P. albicaulis* Engelm.
- Group Flexiles
  - *P. flexilis* James
  - *P. armandi* Franch.
- Group Strobi
  - *P. ayacahuite* Ehr.
  - *P. lambertiana* Dougl.
  - *P. parviflora* Sieb. & Zucc.
  - *P. peuce* Grisebach
  - *P. excelsa* Hook.
  - *P. monticola* Dougl.
  - *P. strobus* L.

SUBSECTION PARACEMBRA

- Group Gerardianse
  - *P. gerardiana* Wall.
  - *P. bungeana* Zucc.
- Group Cembroides
  - *P. cembroides* Zucc.
  - *P. pinceana* Gord.
  - *P. nelsonii* Shaw
- Group Balfourianae
  - *P. balfouriana* Murr.
  - *P. aristata* Engelm.

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In the present paper Shaw's interpretation of section *Haploxylon* is accepted, but twenty-six species are recognized instead of nineteen. The seven additional species result from the elevation to specific rank of several pines that Shaw regards as mere varieties or as synonyms. These additional species are: *P. sibirica* Mayr., *P. pumila* Regal, *P. pentaphylla* Mayr., *P. reflexa* Engelm., *P. monophylla* Torr. & Frem., *P. edulis* Endl., and *P. parryana* Engelm. In the present paper the relationships between these twenty-six species are discussed in the light of their turpentine chemistry.

Of the eleven Old World species of section *Haploxylon,* one occurs in western Europe (*P. cembra*) and one on the Balkan Peninsula (*P. peuce*). One (*P. sibirica*) is essentially a Siberian pine. One (*P. pumila*) occupies the northeastern part of Asia. The remaining seven occur in southeastern Asia. All but one of the fifteen New World species of *Haploxylon* are concentrated in the western part of North America. This one is *P. strobus,* the typical phase of which occurs in the eastern part of the continent while *P. strobus* var. *chiapensis* occurs in the tropical parts of southeastern Mexico (Veracruz, Puebla, Oaxaca, and Chiapas). Thus, most of the white pines occur in southeastern Asia and southwestern North America.

The taxonomy of the Old World pines appears to be relatively simple. An exception is the status of *P. sibirica* and *P. pumila* and perhaps also that of *P. pentaphylla.* On the contrary, the taxonomy of most of the New World white pines is rather confusing. For instance, Shaw's *Pinus cembroides* in our opinion consists of four species: *P. monophylla, P. edulis, P. parryana,* and *P. cembroides.* Apparently there has been a great deal of interbreeding among this group of pines. Another taxonomically ambiguous group is that which is commonly referred to as the Mexican white pine. In reality this group consists of typical *P. ayacahuite,* which, with its two varieties *brachyptera* Shaw and *veitchii* Shaw, grows as far south as Guatemala, and *P. reflexa,* which grows in Arizona, New Mexico, western Texas and has been reported from the states of Chihuahua, Durango, and Nuevo Leon of Mexico.

The author has had the opportunity of studying *P. reflexa* in the Apache Indian Reservation, Arizona. It grows there at an elevation of about 8,000 feet in association with ponderosa pine, Douglas fir, and white fir, with occasional aspen and New Mexican locust underneath. In that locality *P. reflexa* is a tall, straight forest tree which resembles *P. monticola* rather than *P. flexilis,* a "low, thick-trunked much branched tree" (24, p. 7). Sudworth says that "in exposed, higher situations *P. reflexa* has a general resemblance to the limber pine." The synonymy of *P. reflexa* is rather confusing; some botanists call it *P. strobiformis* Sudw. (25, p. 14), others refer to it as *P. ayacahuite* var. *brachyptera* (20, p. 11, pl. 6). According to

Sudworth (24), Engelmann named a variant of *P. ayacahuite* as *P. flexilis* var. *reflexa* and four years later elevated it to the rank of species as *P. reflexa,* a name under which all Mexican white pines were long known to American botanists. In 1889 Sargent (16) pointed out that *P. reflexa* and *P. strobiformis* were synonyms. Little (7) adopts Engelmann's original classification of it, namely *P. flexilis* var. *reflexa.* Dr. Maximino Martinez, a profound student of the Mexican pines, is inclined to follow the later decision of Engelmann and call it *Pinus reflexa* (8), a decision in which we concur. In his "Los Pinos Mexicanos" (8, p. 117), Dr. Martinez displays in a diagram of the section *Ayacahuites,* his concept of the relations of this pine to other closely related white pines. Since *P. monticola* is not known from Mexico, it is not included in Martinez's diagram.

CHEMISTRY

Erdtman (3) and his associates have shown that the section *Haploxylon* differs from the section *Diploxylon* in the composition of the heartwood phenols. Pines of the *Haploxylon* section are characterized by stilbenes and dibenzyls as well as flavones and flavanones derived from phloroglucinol; the group *Strobi,* in addition, contains flavones and flavanones derived from methylphloroglucinol. Monomethyl ether of inositol (pinite or pinitol) is present in all white pines (however, there is very little if any in *P. aristata*).

Pines of the section *Diploxylon* possess stilbenes but not corresponding dibenzyls; flavanones are present but flavones are not. Pinitol is absent. The two sections are thus clearly distinguishable from each other biochemically. Unfortunately a further subdivision based on the heartwood phenols is possible only in a few cases.

In the present paper the author endeavors to discuss the chemical composition of the turpentines of the white pines (Pinus, section *Haploxylon*). However, it must be pointed out that the chemical picture is not yet complete. There are still eight pines in which the turpentines have not been analyzed. Some of these pines (*P. armandi, P. bungeana*) are difficult of access; and it appears that their turpentines may remain unknown for some time.

It is not the author's intention to devise a chemical classification for pines that would replace the existing morphological classification. The purpose of this paper is merely to show that there are spheres of chemical relationship among different pines. This information along with other evidence may be used by botanists when the taxonomy of pines is revised.

Turpentine is the volatile part of oleoresin, or pitch, of pines and other conifers. It is not a pure chemical substance but a mixture of several chemical compounds, mostly terpenes ($C_{10}H_{16}$).

A major component of all pine turpentines is alpha-pinene. In the section *Haploxylon* only *P. albicaulis* lacks this turpene (6); all other white pines possess varying amounts of alpha-pinene, in some species up to 98 percent of the total amount of turpentine. Other terpenes—beta-pinene, limonene, delta-3-carene, terpinolene—occur in some white pines in smaller quantities. Sesquiterpenes ($C_{15}H_{24}$) occupy a subordinate position; these are important in determining chemical relationships of the pines. Oxygen-containing terpene derivatives are rare and probably often of a secondary origin (oxidation during collecting, storing, and distilling the oleoresin).

Very interesting is the occurrence of saturated straight chain hydrocarbons, heptane (C_7H_{16}) and undecane ($C_{11}H_{24}$), in several white pines. These hydrocarbons are found also in some *Diploxylon* pines: ninety-five percent of turpentines of *P. Jeffreyi* and *P. sabiniana* consists of n-heptane.

All *Haploxylon* pines and the chemistry of the turpentines of most of them are represented diagramatically in fig. 1. Solid line circles denote those pines whose turpentines have been investigated; broken line circles represent the pines that have not yet been investigated. Rectangular boxes indicate groups of pines possessing a similarity of chemical composition of their turpentines. Solid lines indicate chemical relationship between different pines. Broken lines suggest a possible relationship. Numbers in parentheses refer to the literature references listed at the end of the article.

In considering the turpentine chemistry of the white pines, we should keep in mind that the present composition of the section *Haploxylon* is probably very different from the composition of its progenitors in previous geological periods. Pines probably originated during the Permian period, and the *Haploxylon* pines were separated from the *Diploxylon* pines very early in history, perhaps during the Jurassic. No living species of pine occur in deposits older than those of Miocene (9), so we may assume that many connecting links between different pines have been lost in the past. For instance, the presence of saturated hydrocarbons in some pines is probably of a very ancient origin, and it is possible that in the past geological periods there were more pines containing saturated hydrocarbons than now (23). Most such pines apparently disappeared long ago.

Saturated carbons, which rarely occur in contemporary pines, are found in the following four species of the group *Strobi*: *P. excelsa*, *P. monticola*, *P. reflexa*, and *P. ayacahuite*. Undecane was discovered in *P. excelsa* of India by Simonsen and Rau (23). Later this hydrocarbon was found in *P. monticola* (4) and in some hard pines. *Pinus reflexa* (13) contains two saturated hydrocarbons, undecane and heptane, and a sesqui-

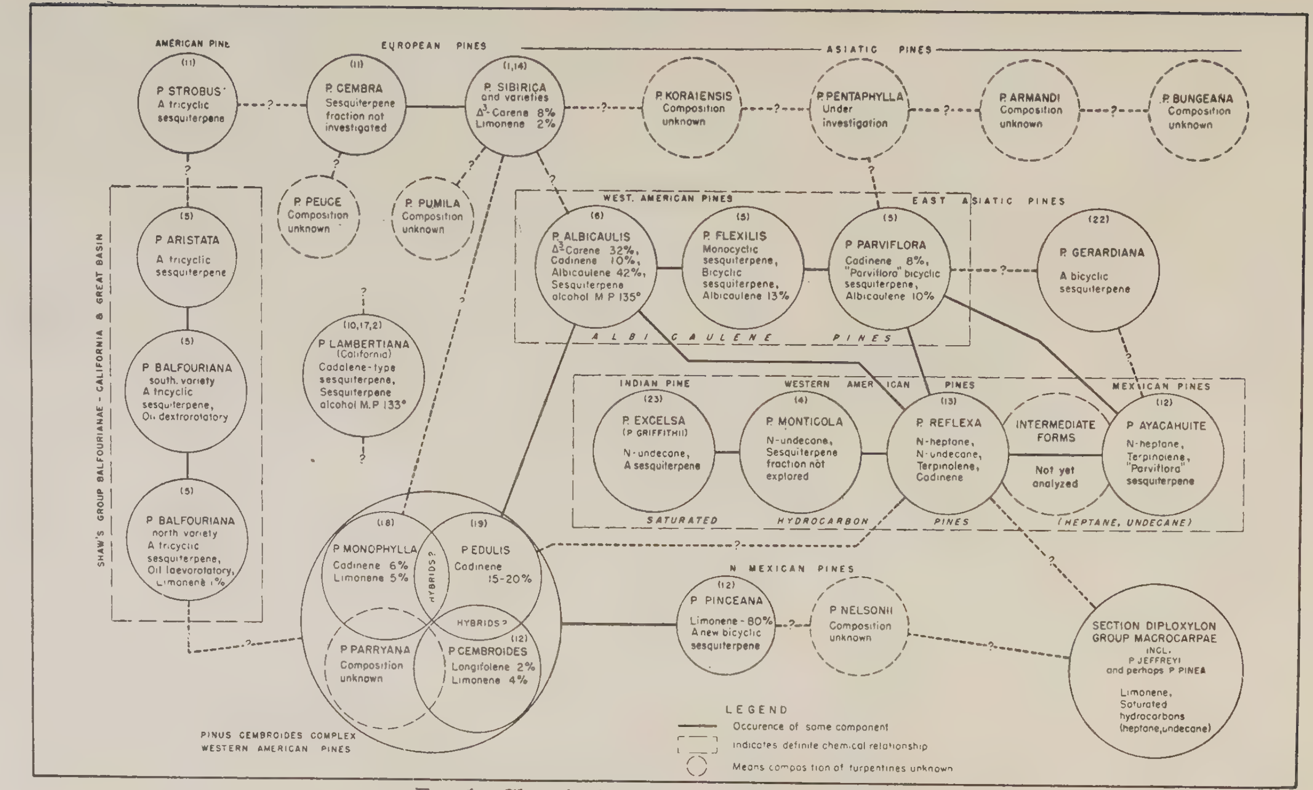

FIG. 1. Chemical relationship of white pines.

terpene—cadinene. The fourth species of this chemical group, *P. ayacahuite,* possesses heptane but no undecane (21).

A bicyclic sesquiterpene occurring in *P. ayacahuite* is apparently identical with the sesquiterpene of *P. parviflora.* The presence of a bicyclic sesquiterpene in *P. gerardiana* (22) of Kashmir and Afghanistan suggests a chemical relationship of this pine to *P. ayacahuite* on one hand and to *P. parviflora* on the other.

The presence of n-undecane in *P. lambertiana,* reported by Schorger (17), has not been substantiated by more recent studies (10). This pine is difficult to cross with other white pines and it stands alone in chemical composition of turpentine. It is an endemic pine of California and Oregon, but apparently, judging by the physical constants of its turpentine, it possesses a considerable variability (2), and should be studied more intensively. It might be possible that its sesquiterpene alcohol (melting point 133° C.) is identical with the sesquiterpene alcohol of *P. albicaulis.*

Pinus albicaulis occupies a unique position among the white pines. Morphologically it is grouped with *P. cembra, P. sibirica, P. pumila,* and *P. koraiensis.* The chemistry of its turpentine is the most complicated of all white pines linking it not to those species with which it is morphologically related, but to others. *Pinus albicaulis* turpentine contains a diterpene, and appreciable amounts of a sesquiterpene, albicaulene (6), the latter being found also in the turpentines of *P. flexilis* and *P. parviflora* (5). On the other hand its turpentine contains a sweet-smelling terpene, delta-3-carene, which is also found in *P. sibirica,* but is rare in other white pines. The presence of a sesquiterpene, cadinene, in *P. albicaulis* turpentine suggests a relationship of this pine with the *P. cembroides* complex.

Pinus cembra (11) and related Eurasian pines shown on the top of the chart (fig. 1) have not been adequately studied. Nevertheless, it is evident that *P. cembra,* an alpine species of western Europe, is chemically different from the Eurasian *P. sibirica.* The latter pine, occupying an extensive area from Kola peninsula in northwestern Russia to beyond Lake Baikal in eastern Siberia, possesses several morphologically different varieties (such as *P. coronans* Litw.) as well as chemically different varieties (14, 1). *Pinus pentaphylla* is now under investigation, but the two extremely interesting southeastern Asiatic species, *P. armandi* and *P. bungeana,* still remain unknown. It is to be expected that their turpentines are rather complicated.

Pinus aristata and *P. balfouriana* belong, according to Shaw (21) to group *Balfourianae,* the foxtail pines. This group is represented on the left side of the chart (fig. 1). Chemically as well as morphologically these two pines have a great deal in common. The harmonious picture is slightly complicated by our finding that *P. balfouriana* from northern California is somewhat different from the disjunct population in the southern Sierra Nevada. The northern locality is west of Mount Shasta; the southern locality is not far from Mount Whitney. The two localities are separated (and probably have been since before the Pleistocene) by a distance of 400 miles. We have studied turpentines from the two localities (5) and have found that both of them contain a tricyclic sesquiterpene, but that the turpentine from the northern location contained some beta-pinene and limonene, while that from the southern location lacked these components but contained some bornyl acetate. Both turpentines consist mainly of alpha-pinene, but in the northern location there was predominance of a laevorotatory antipode of this terpene while in the southern location, a dextrorotatory antipode prevailed. *Pinus balfouriana* is a pine of alpine environment and its two populations, the northern and the southern, have not been compared closely by botanists. It is generally assumed, however, that pines from the two localities are morphologically identical.

Although there is a very close relationship between the two populations of *P. balfouriana,* the chemical composition of their turpentines indicates that there are noticeable and important differences perhaps not yet perceptable to the human eye, but easily detectable by the precise laboratory instruments. Since the geographic separation of the two populations, some changes have taken place which now distinguish them. We are witnessing here, perhaps, a step in the origin of a new species.

Pinus aristata (5) is closely related chemically to both forms of *P. balfouriana.* It is not certain if the tricyclic sesquiterpene of *P. aristata* is the same as the tricyclic sesquiterpene of *P. strobus.* Nevertheless, it is significant that the latter pine also possesses a tricyclic sesquiterpene.

Of the four pines constituting the *P. cembroides* complex, one species, *P. parryana,* has not yet been investigated. *Pinus monophylla* has cadinene and limonene in its turpentine, the latter a terpene relatively rare in white pines. Cadinene is also found in *P. edulis,* but no limonene. While the percentage of cadinene in typical *P. monophylla* of western Nevada is rather small (6 per cent), it apparently increases eastward, and in Utah, where *P. monophylla* apparently crosses with *P. edulis,* cadinene may reach fifteen percent of the total weight of turpentine.

Pinus cembroides has no cadinene but another (tricyclic) sesquiterpene, longifolene, which occurs in some hard pines (*P. torreyana* of the group *Macrocarpae,* and *P. roxburghii* of the group *Longifoliae*) and in some other Asiatic pines. Limonene also occurs in *P. cembroides,* indicating a closer affinity between *P. cembroides* and *P. monophylla* than between *P. cembroides* and *P. edulis.* In *P. pinceana* a new (bicyclic) sesquiterpene appears. This pine belongs along with the *P. cembroides* complex to the group *Cembroides*, the desert nut pines of southwestern North America. *Pinus pinceana* turpentine is outstanding in being composed mostly of limonene. The chemistry of the turpentine of *P. Nelsonii* is not yet known. It must have an interesting composition.

The chemical picture of the *P. cembroides* complex is thus very similar to the botanical picture as suggested by Martinez in his "Los Pinos Mexicanos" (8, p. 117), while the presence of large quantities of limonene in *P. pinceana* links the group *Cembroides* with the group *Macrocarpae* of Section *Diploxylon*. (Limonene in large quantities is also found in *P. pinea*, *P. serotina* and in *P. lumholtzii*.) On the other hand, the presence of the saturated hydrocarbons of the *Macrocarpae* pines suggest their relation to *P. reflexa* and other white pines containing these hydrocarbons.

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A NEW SPECIES OF CLARKIA (ONAGRACEAE)

Harlan Lewis and W. R. Ernst

Clarkia similis sp. nov. Herba erecta altitudine ad 9 dm.; caulibus simplicibus vel ramosis; foliis angusto-lanceolatis vel elliptis, denticulatis, 2–4 cm. longis, 3–8 mm. latis, in basi ad petiolos usque ad 8 mm. longo angustatis; inflorescentium axe in apice recurvato; calycis tubo 1.5–2 mm. longo, annulo pilorum ad apicem posito, limbo 6–10 mm. longo, circiter 1.5 mm. lato; petalis 6–12 mm. longis, 3–6 mm. latis, oblanceolatis vel rhomboideis vel obovatis subintegris, acutis vel rotundatis, in basi in unguiculum gracilis circiter 1 mm. longum angustatis, albis vel pallidis in parte inferior purpureo-punctulatis; staminibus 8, plerumque ab stigmate liberis; stigmate quadrifido, lobis brevibus; stylo aequante stamines; ovario 8-canaliculato, 1.5–2.5 cm. longo; capsula 1.5–3 cm. longa, 1–1.5 mm. lata.

Erect herb as much as 9 dm. tall; stems simple or branched, puberulent above with short upwardly curled hairs sometimes sparsely so, sparsely puberulent to glabrate below; leaf blades narrowly lanceolate to lanceolate-elliptic, subentire to denticulate, 2–4 cm. long, 3–8 mm. broad, the apex often obtuse, glabrate to sparsely puberulent, narrowed into petioles as much as 8 mm. long; rachis of the inflorescence reflexed in bud becoming erect as the flowers open; buds pendulous; hypanthium 1.5–2 mm. long, puberulent, the ring of hairs at the upper margin; sepals lanceolate 6–10 mm. long, about 1.5 mm. broad; petals 6–12 mm. long, 3–6 mm. broad, oblanceolate to rhomboid or obovate, subentire, the apex rounded, acute or undulate, narrowed at the base to a slender claw about 1 mm. long, nearly white to light pink shading to white below, flecked with purple in the lower half; stamens 8, in two series, the outer longer, both series with yellowish pollen; anthers usually free from the stigma; stigma whitish with 4 short lobes; style pinkish, equaling the stamens; ovary subterete, 8-striate, 1.5–2.5 cm. long, sessile or on pedicels as much as 3 mm. long; mature capsules quadrangular 1.5–3 cm. long, 1–1.5 mm. broad.

Type. 7.6 miles west of Ramona, San Diego County, California, April 22, 1951, *Lewis, Lewis, Ernst and Mathias 773* (UCLA).

Distribution. California: Fresno, Los Angeles, Orange, Riverside, San Benito, San Bernardino and San Diego counties. Probably also in northern Baja California.

Specimens examined. Fresno County: 12 miles from Coalinga on the road to Parkfield, *Eastwood and Howell* in 1938. Los Angeles County: Wolfskill Canyon off San Dimas Canyon, *Ewan 2376;* East Fork of Big Santa Anita Canyon, San Gabriel Mountains, *Howell 3777.* Orange County: Santa Ana Mountains, San Juan Canyon, 0.2 mile west of Upper San Juan Camp Ground, *Lewis, Lewis, Ernst & Mathias 769*, Santa Ana, *Smith* in 1930. Riverside County: Cranston Ranger Station, San Jacinto Canyon, without collector in 1951; Banning, *Gilman 23;* 10 miles south of Hemet, *Munz 10816;* Elsinore, *McClatchie* in 1892; San Juan Mountains, San Juan Canyon, *Winblad* in 1941. San Benito County: Pinnacles, *Howell 12936*. San Bernardino County: Arrowhead Hot Springs, *Grant 6617;* mountain slopes, Clear Creek road, *Parish* in 1891; San Diego County: *Cooper 531; Henshaw 27;* San Diego, *T. S. Brandegee* in 1903; top of the grade, Descanso, *K. Brandegee* in 1906; Fallbrook, *Cleveland* in 1981 (sic!); Ramona, *Collins and Kempton 159;* Warner's Springs, *Coombs* in 1911; Tia Juana, *Eastwood 2929;* South Fork Featherstone Creek, Barona Valley, *Gander 4015;* 3 miles south of Deluz, *Gander 5793;* Burn between Campo and Canyon City, *Gander 9346;* 5 miles south of Mesa Grande, on Black Canyon Road, *Gander 11356;* San Diego, *Grant 88;* Potrero Grade, *Gray* in 1925; San Ysabel, *Henshaw* in 1893; San Felipe Creek, *Keck and McCully 111;* 7.6 miles west of Ramona, *Lewis, Lewis, Ernst and Mathias 773* (type); Banner Grade below Julian, *Munz and Hitchcock 11363.*

The haploid chromosome number is 17. Material from the type collection has not been counted. The count is based upon examination of pollen mother cells of the following collections: Orange County: Santa Ana Mountains, San Juan Canyon, 0.2 mile west of Upper San Juan Camp Ground, *Lewis, Lewis, Ernst and Mathias 769.* San Benito County: High Peaks Trail, Pinnacles National Monument, *Lewis and Epling 787* (approximately 17 pairs, no definite count). San Diego County: 0.4 mile east of Cleveland National Forest boundary on road to Barret Lake, *Lewis and Lewis 277;* 2.1 miles east of Cleveland National Forest boundary on road to Barret Lake, *Lewis and Lewis 280;* Campo to Potrero road between culverts D 8.07 and D 8.14, *Lewis and Lewis 288A.* Permanent slides and herbarium vouchers are on file at the University of California, Los Angeles.

Clarkia similis is a tetraploid species (n=17) which on morphological grounds is most closely related to *Clarkia modesta* Jeps. (n=8) and *Clarkia epilobioides* (Nutt.) Nels. & Macbr. (n=9) and probably represents an allopolyploid derived from them. The nature of the chromosome pairing in the hybrid *C. modesta* × *C. similis* and that of the hybrid *C. epilobioides* × *C. similis* leaves very little doubt that this hypothesis is correct. The hybrid between *C. modesta* and *C. epilobioides* is morphologically similar to *C. similis.*

Clarkia modesta, C. epilobioides and *C. similis* are morphologically so similar that Hitchcock (revision of North American species of *Godetia.* Bot. Gaz. 89:321–361. 1930) included all of them within a single species (*Godetia epilobioides*) without even subspecific recognition. The reason is not difficult to find. All three species are very similar vegetatively and differ primarily in the color and conformation of the corolla. The flowers of *C. epilobioides* are uniformly bright white or somewhat yellowish, often pink in age. The petals are obovate and uniformly arranged forming a regular corolla. The petals of *C. modesta* on the other hand are oblanceolate or somewhat rhomboid, pink, usually with darker flecks in the lower half, and are usually not equally spaced but are arranged in lateral pairs. The petals of *C. similis* are more or less intermediate, usually pale pink or sometimes nearly white and normally flecked. The petals are more variable in shape than in either diploid species and the flowers are usually somewhat irregular. Viewed only from herbarium sheets, without knowledge of the chromosome complements, the three species present a complex picture suggesting continuous variation in a single polytypic species. However, once the basis of genetic discontinuity is apparent the morphological discontinuity between living populations becomes obvious, particularly where two of the species are found growing together.

The distribution of *C. similis* between southern California and the Pinnacles region in San Benito County is apparently disjunct. It is uncertain at present whether these two races, which differ somewhat morphologically, represent independent origins of the allopolyploid or segregation from a once continuous distribution. *Clarkia epilobioides,* but not *C. modesta,* often occurs with *C. similis* in southern California. Both diploids are found in the area of *C. similis* in San Benito County.

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We are indebted to Professor Carl Epling for assistance with the Latin diagnosis.

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MORPHOLOGICAL CRITERIA FOR THE SPECIFIC VALIDITY OF PINUS JEFFREYI

DONALD A. JOHANSEN

The validity of *Pinus jeffreyi* Murr. as a distinct species has long been in dispute among taxonomists. Some (1, 2, 3, 7) recognize it as distinct; others consider it to be a variety of *P. ponderosa* Dougl. (5, 9); while still others give it no recognition whatever (10, 11). Those who reduce *P. jeffreyi* to varietal rank have apparently been disturbed by the fact that "intermediate" or "intergrading" forms are rather common in certain regions where the two species or others occur more or less intermingled. It was not until comparatively recently that it came to be realized that these "intergrades" are actually natural hybrids. Several such hybrids have been experimentally produced (4, and personal communications from Dr. Duffield).

Mirov (8) accepted the distinction between the two species on biochemical grounds and concluded that *P. jeffreyi* is phylogenetically older than *P. ponderosa.* In the latter conclusion, he agrees with the opinion of Lemmon (6).

For several years the writer has been conducting an intensive and extensive investigation of archegoniogenesis in the genus *Pinus* and other gymnosperms. Among other results, it was ascertained that the account of events within the archegonium, which has prevailed for the past fifty years, was incomplete. This story actually concerns only the almost entirely modern, evolved archegonium in a single species (the so-called

"*P. laricio*," whose true identity is now considerable of a mystery; it seems to have been a cultivated hybrid). Again, it was determined that each valid species possesses a mode of archegoniogenesis peculiar to itself; no two species out of twelve so far investigated follow the identical procedure. No species is wholly archaic nor entirely modern in all characteristics; in a given species certain archaic features are retained but all others are modern. It is the variation in the degree to which archaic features are retained that distinguishes any one species from the others. Consequently, a tabulation of all the archegonial characteristics prevailing in a given species serves as a reliable criterion for indicating differences between that species and any other species. Comparison of one character after another in each species reveals that *P. jeffreyi* differs so markedly from *P. ponderosa* that the only possible conclusion is that the former is a valid species.

In the following tabulation those characters known or at least presumed to be archaic are printed in italics.

Archegonial Character	*Pinus ponderosa*	*Pinus jeffreyi*
Number of archegonia	4 in very narrow ovules; 8 *in all others*	2 in narrow ovules 4 in wider ones
Location	*When 8, always in a complex*	Never in a complex
Shape	*Globoid to ovoid*	Laterally hemispheric
Neck cells	*Flush with outer cells of gametophyte and laterally elongated*	Deeply buried in gametophyte and vertically elongated; tending to obliteration
Jacket cells	Well developed	Poorly developed
Archegonial beak	Present	*Absent*
Chromatin elimination nucleus ("ventral cell") cut off	July 8-10; small; terminal	June 2-5; conspicuous; lateral; sometimes all chromatin is eliminated
Nuclear state	Always single; small	*Commonly binucleate* (two mitoses in place of one); quite large when single

Fertilization	Always single	*Always double when binucleate;* otherwise single
Syngamy occurs	July 20	June 10-12
Cytoplasm	*Turgid and highly vacuolate; does not plasmolyze*	Not turgid; few or no vacuoles; dense; always plasmolyzed after all killing fluids
Proteins or other stainable foods	*Absent*	Abundant and deeply stained
Nuclei in mature free-nucleate proembryo	Four	*Eight after double fertilization;* otherwise four
Reversion to Araucarian type of proembryo (walled)	Absent, or at least never observed	*Rather common*

Other interesting morphological features have turned up in other species but not in *P. jeffreyi* or *P. ponderosa;* they need not be mentioned here but they are useful in distinguishing these two from other species.

The ovules of *P. jeffreyi* are much larger than those of *P. ponderosa.* It is significant that binucleate archegonia, double fertilization and the tendency to revert to the ancestral (Araucarian) type of proembryo characterize species with large seeds (such as *P. lambertiana*), and that these features tend to disappear gradually as the ovules decrease in size until mostly evolved characters prevail in those species with the smallest seeds (as in *P. banksiana*). Large seeds occur in the cycads, *Ginkgo* and the Araucarians; the writer has recently found binucleate archegonia with double fertilization in *Zamia floridana,* as well as plurinucleate archegonia in *Ginkgo biloba* and twin proembryos in *Araucaria angustifolia.*

Natural hybrids in Pinus are still much of a morphological puzzle; the writer began to investigate them only during the past year. They are especially abundant in the region between Mountain Center and Idyllwild in the San Jacinto Mountains, with only *P. jeffreyi* occurring at the Mountain Center end and *P. ponderosa* at the Idyllwild end, with the hybrids in between and with numerous trees of *P. coulteri* and fewer of *P. flexilis* intermingled. Most of these hybrids more closely resemble *P. jeffreyi* in habit than they do *P. ponderosa,* but their archegoniogenesis resembles that of neither species. The suspicion, already voiced by others, is strong that *P. coulteri* has had something to do with the origin of these hybrids. Moreover, at the far upper end of San Antonio Canyon, in the San Gabriel Mountains, there are numerous trees which have long been presumed to represent *P. ponderosa*, but their archegonial characters are so radically different from those of this species that they are either hybrids or constitute an unrecognized species. *Pinus lambertiana* is the only other species native to the neighborhood.

Mainly because of the presence of binucleate archegonia and double fertilization, together with the formation of Araucarian-like proembryos, all of which are pronouncedly archaic features, the writer is convinced that *P. jeffreyi* is the older species and therefore agrees with the conclusions of Lemmon and Mirov.

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REVIEW

A Natural History of Western Trees. By DONALD CULROSS PEATTIE, illustrated by Paul Landacre. Houghton Mifflin Company, Boston, Mass. pp. xiv + 751, 4 maps (inside covers), 39 plates, 164 text figures. 1953. $6.00.

It is hard to avoid superlatives in reviewing this handsome volume and, after all, why avoid them when they are so well-merited? Considering the wealth of information it conveys and its profuse and attractive illustration, it is a real bargain at the price fixed by the publishers. Anyone who is at all interested in trees will find that he is getting more than his money's worth when he purchases this book. Others who are not particularly concerned with trees, as such, will enjoy the work as literature of a high order. The author's name is sufficient guarantee of this.

The territory covered is bounded on the east by Meridian 100, on the west by the Pacific Ocean, on the north by the Arctic Ocean and on the south by the Mexican Boundary. As to the always troublesome question of what constitutes a tree, the author states in his Foreword: "True that no perfectly satisfactory definition separates trees clearly from shrubs; the sharper one tries to make such a distinction, the more absurdities and contradictions one raises. In general, however, the author has fought to keep out of the book as many shrub-like species as possible, in order to let the trees rise clear."

As a rule, the distinction has been made consistently, but one wonders why *Ptelea, Fremontia,* and *Garrya* were omitted when two species each of *Ceanothus* and *Arctostaphylos* are included.

About 200 species are described, some at considerable length (a dozen or more pages), others in only a paragraph or two. Nearly all of these are illustrated by skillfully drawn text figures, a few also by full-page plates. The great importance of the Coniferae in western forests is shown by the fact that two-fifths of the descriptive portion of the text is devoted to this class.

There are given, under each species, the scientific and popular name, or names, the geographical range, and a botanical description, followed by a less formal account of the tree in its various aspects. Economic uses, if any, are treated, often quite fully. No one has written more convincingly of the important role of trees in the history and economy of the West, both aboriginal and recent. Certainly no one has given us more enchanting descriptions of the beauties peculiar to each species. Personal observations by the author during his extensive travels in the West have supplemented the information obtained from the literature, and this is reflected in the vividness of the descriptions.

The chapters on the Giant Sequoia, Coast Redwood, Sugar Pine, Douglas Fir, Monterey Pine, Valley Oak, and Western Sycamore may be mentioned as outstandingly interesting but, in fact, the whole book may be read with delight. Desert-lovers will enjoy the accounts of the Desert Palm (*Washingtonia*), Joshua Tree (*Yucca*), Mesquite (*Prosopis*), Desert Smoketree (*Dalea*), Desert Ironwood (*Olneya*), Elephant-tree (*Bursera*), and Saguaro (*Carnegiea*).

The book concludes with general keys as well as special keys to the species of the larger genera (*Pinus, Quercus,* etc.), a glossary, and separate indices of scientific and common names. In the botanical descriptions in the text, as well as in the keys and glossary, the terminology is simplified as much as possible. For this reason, and with the aid of the excellent illustrations, it should be possible for those who have had no formal botanical training to identify most of the western trees without much trouble.

Mr. Peattie, in his Foreword, mentions the many happy years he has devoted to this undertaking. He is to be congratulated on the splendid book that is the outcome of these congenial labors.—T. H. KEARNEY. California Academy of Sciences, San Francisco.